A REVIEW OF GYNANDROMORPHISM IN THE GENUS *ORNITHOPTERA* BOISDUVAL, (LEPIDOPTERA: PAPILIONIDAE)

J. E. NIELSEN

GPO Box 858, Canberra, ACT 2601

Abstract

A review of records of gynandromorph specimens in the genus *Ornithoptera* Boisduval is presented, with the causes of gynandromorphism in insects briefly discussed. Most *Ornithoptera* gynandromorphs are known from *O. priamus* (Linnaeus), which probably reflects the number of specimens available as opposed to an unusual tendency towards gynandromorphism in this species. Gynandromorphs are also known of *O. croesus lydius* (Felder), *O. victoriae regis* (Rothschild), *O. goliath* Oberthür, and the Australian taxa *O. priamus pronomus* (Gray), *O. richmondia* (Gray) and *O. euphorion* (Gray).

Introduction

A gynandromorph is an organism whose genotype simultaneously expresses aspects of both male and female morphology in the phenotype. Gynandromorphism is generally attributed to genetic errors associated with cell division, with different errors at different stages of development believed to produce different types of gynandromorph (Pereira *et al.* 2003, Richards and Davies 1977, Wigglesworth, 1972). Gynandromorphs are exceedingly rare in nature and are only obvious where there is strong sexual dimorphism. The phenomenon has been most commonly observed in insects, where the phenotypic expression of sexual difference is not mediated by the prevailing endocrine environment. Gynandromorphism has also been recorded in birds, where other processes have been postulated, including the suggestion that sex chromosome genes acting within individual cells directly contribute to sex differences in cell function (Agate *et al.* 2003).

The precise mechanism leading to gynandromorphism is not well understood in butterflies, in which sex is determined by a WW/WZ system, with the heterogametic sex (ie WZ) being the female, the reverse of the condition found in mammals and most other insects. It is better understood for the *horka* mutation of the vinegar fly *Drosophila melanogaster* (Meigen, 1830) (Szbad *et al.* 1995). All known mechanisms of *Drosophila* gynandromorphism rely on the zygote (fertilised egg that has not yet undergone division or cleavage) having an initial chromosome component of $X^{Y}X$ (male), and subsequent loss of the X chromosome.

In *D. melanogaster*, the *horka* mutation produces gynandromorphs due to nondisjunction, where chromosome inheritance to 'daughter' cells is inhibited. For *horka*, all chromosomes except X^{Y} are unreliably inherited during cleavage and subsequent cell divisions producing the blastula (Szbad *et al.* 1995). If the X chromosome is not inherited by one of the cells produced at cleavage, its absence will likewise be inherited by all 'daughter' cells. As the two cells produced at cleavage subsequently proliferate into what later become the lateral halves of the adult organism, this type of error

may ultimately produce a phenotype whose lateral halves are of opposite sex (bilateral gynandromorph). Localised loss of the *X* chromosome later in development is also believed to produce gynandromorphs whose phenotype is a mosaic of both male and female morphology (Richards and Davies, 1977; Wigglesworth 1972) (mosaic gynandromorphism).

Additional causes of gynandromorphism in insects include fertilisation of binucleate ova, replacement of mitotic cell division with meiosis and fertilisation by multiple sperm, which may fuse and act as a second nucleus (Pereira *et al.* 2003, Richards and Davies 1977, Wigglesworth 1972).

Gynandromorphism in *Ornithoptera*

Ornithoptera Boisduval, 1832 is a genus of thirteen species of swallowtail butterflies restricted to the Australasian biogeographic region (ie. east of Wallace's line) (Parsons 2000). Three species, *O. richmondia* (Gray, 1852), *O. euphorion* (Gray, 1852) and *O. priamus* (Linnaeus, 1758), occur within Australian territories (Braby 2000). Along with two additional genera (*Trogonoptera* Rippon, 1890 and *Troides* Hübner, 1819), the *Ornithoptera* are popularly known as birdwings and have attracted considerable scientific interest in the areas of taxonomy (e.g. Hancock 1983; 1991; Braby *et al.* 2005), conservation ecology (Collins and Morris, 1985, Sands *et al.* 1997, Sands and New 2002) reproductive biology (Orr, 1988) and general ecology (Matsuka 2001, Parsons 2000). As this genus includes some of the largest and most spectacular of all Lepidoptera, they are much prized by amateur collectors (Collins and Morris, 1985). All species (excluding *O. alexandrae* (Rothschild, 1907)) are presently bred in ranching programs, with large numbers sold internationally to collectors. Trade in these species is monitored under Appendix 2 of the Convention on the International Trade in Endangered Species (CITES) (United Nations Environment Programme, World Conservation Monitoring Centre, 2007).

Ornithoptera is an ideal genus to review for gynandromorphs as all species exhibit spectacular sexual dimorphism, such that extremely small areas of male tissue may be visible on a female wing, and vice versa. Moreover, the trade in aberrant *Ornithoptera* results in a high rate of reporting (if only in sales catalogues) and there is extensive literature describing and illustrating even the slightest variations observed in most species (e.g. D'Abrera 2003; Otani and Kimura 2001, Schäffer 2001). A thorough review of literature yielded a large number of *Ornithoptera* gynandromorph records, which are presented in Table 1. Only specimens clearly identified as natural gynandromorphs are presented because some fraudulent material has been 'manufactured' and advertised for sale on the internet in recent years (eg. a purported *O.* x *allottei* (Rothschild, 1914) gynandromorph, consisting of the body and left wings of a female *O. victoriae regis* (Rothschild, 1895) with the right wings of a male *O. priamus urvillianus* (Guérin-Méneville, 1830)). Elements of the *Ornithoptera* wing pattern defined by Haugum and

Low (1978) are used to describe the gynandrous phenotype of individual specimens. *Ornithoptera* taxonomy used here follows that presented by Parsons (2000) and Braby (2004).

Fig. 1 Mosaic gynandromorph of *O. priamus pronomus* collected by H. Elgner at 'Cape York', Queensland, on 17 February 1907. Specimen in the Australian Museum. above: upperside, below: underside.

Table 1. List of known *Ornithoptera* gynandromorphs, including for each specimen, collection locality, gynandromorph type, description of phenotype, literature references and current repository. Abbreviations: LH (left half); RH (right half); FW (forewing); HW (hindwing); D (dorsal wing surface); V (ventral wing surface); AM (Australian Museum); British Musuem (Natural History) (BM(NH)); IFTA (Insect Farming and Trading Agency, Papua New Guinea); P (various private collections).

Species Group Taxon	Locality	Type	Phenotype	Reference and Repository
euphorion	Australia (Kuranda, Queensland)	Mosaic	♂ overall with ♀ scaling on RH FW and HW. Halved genitalia.	Schäffer (2001) P
richmondia	Australia (Queensland?)	Mosaic	♀ overall with partial ♂ radial band on RHFW apex.	Sands and Scott 2002 Photograph only
priamus pronomus	Australia ('Cape York', Queensland)	Mosaic	Figure 1.	Common and Waterhouse 1972 (as *O. priamus poseidon*) AM:
priamus admiralitatus Rothschild, 1915	Papua New Guinea (Trobriand Isl.)	Bilateral	LH male, RH ♀; abdomen bilaterally divided.	Haugum and Low 1978 P
priamus admiralitatus	Papua New Guinea (Admiraly Is.)	Bilateral	Not figured; LH ♂; Received by IFTA.	Parsons 2000 Not specified
priamus poseidon	New Guinea (no locality)	Bilateral	LH ♂, RH ♀; abdomen bilaterally divided.	D'Abrera 2003 BM(NH)
priamus poseidon	Papua New Guinea (Aseki, Morobe Province)	Mosaic	LH ♂ w. ♀ scaling on HWV; RH ♀ w. ♂ scaling on HW. Abdomen w. ♂ genitalia, mostly ♀ dorsally, mostly ♂ ventrally.	Otani and Kimura 1998; Matsuka 2001 P

Table 1 continued

Species Group Taxon	Locality	Type	Phenotype	Reference and Repository
priamus poseidon	Papua New Guinea (Aseki, Morobe Province)	Mosaic	Predominantly ♂; RHFW mostly ♀ w. partial ♂ radial band; LH ♂ w. ♀ scaling on HW tornus and FW apex.	Matsuka 2001 P
priamus poseidon	Indonesia (Nabire, Papua province)	Mosaic	Predominantly ♀; FW w. partial ♂ radial streak and evidence of black median stripe. Overall markings diffuse w. much iridescence.	Otani and Kimura, 1998 P
priamus urvillianus	Papua New Guinea (Bougainville province)	Mosaic	LH ♀; RH ♂ w. limited ♀ scaling on HW. ♀ abdomen w. ♂ scaling. Ranched.	Parsons (1999) IFTA
croesus lydius	Indonesia (Halmahera Is.)	Bilateral	LH ♂, RH ♀; abdomen bilaterally divided.	Parrott and Schmid, 1984 (in Parsons 2000) P
victoriae regis	Papua New Guinea (Bougainville province)	Mosaic	FW generally ♂ with ♀ markings; HW ♂ with ♀ pattern and ♂ scaling.	D'Abrera 2003 Howarth 1977 BM(NH)

Several *Ornithoptera* gynandromorphs that lack a formal literature reference but are otherwise well known to collectors via the internet are also presented. They are listed separately to those discussed in literature (Table 2). Specimens of female *O. priamus poseidon* and *O. aesacus* with iridescence on the wings not taking the form of defined markings are not considered to be gynandromorphs.

Australian *Ornithoptera* gynandromorphs

Of the three known Australian *Ornithoptera* gynandromorph specimens, only one resides in an Australian collection. This specimen, a mosaic gynandromorph of *O. priamus pronomus* (Figure 1), was collected at 'Cape York', Queensland, by H. Elgner on 17 February 1907. It is currently lodged

in the Australian Museum. This specimen was incorrectly referred to as a specimen of *O. priamus poseidon* (Doubleday, 1847) by Common and Waterhouse (1971). A gynandromorphic specimen of *O. euphorion* held in a private collection in Germany was figured on both surfaces by Schäffer (2001) and is described as originating from Kuranda, Queensland. It is most likely a captive bred specimen. A second, bred mosaic gynandromorph of *O. euphorion* is also known and will be discussed in a forthcoming article

A gynandromorph of *O. richmondia* figured by Sands and Scott (2002; pages 8 & 46) was predominantly female with a partial male radial band. It does not appear to have been collected and was not recognised in text as a gynandromorph by Sands and Scott (2002). The provenance of this photograph was not cited.

Table 2. *Ornithoptera* gynandromorphs sighted via the internet with no literature reference ('anecdotal' records).

Taxon	Locality	Type	Phenotype
goliath	Indonesia (Papua province)	Mosaic	Predominantly ♀; RHFW mostly ♂ w. slight ♀ influence; LHFW w. partial ♂ radial band. Ranched.
goliath	Indonesia (Papua province)	Mosaic	♀ w. partial ♂ cubital band on LHFW. Ranched.
goliath	?	Bilateral	LH ♂, RH ♀.

Other notable *Ornithoptera* gynandromorphs

Ornithoptera gynandromorphs have also been reported for *O. priamus, O. croesus lydius* (Felder, 1865) and *O. goliath* Oberthür, 1888, with the majority of specimens known from *O. priamus* subspecies (Appendix 1). The higher frequency of gynandromorphs for the latter taxa probably reflects its abundance through much of its natural range (Parsons 2000) and the quantity of specimens collected for trade, as opposed to a genuinely higher frequency of gynandromorphism. Trade in *O. priamus* subspecies represent some 47% of all *Ornithoptera* trade monitored by CITES, with at least 158,369 specimens exported from Indonesia, Papua New Guinea and the Solomon Islands between 1985 - 2005 (United Nations Environment Programme, 2007).

Three gynandromorphs of *O. goliath* were also examined from a series of detailed photographs published on the internet between 2001 - 2010 (Appendix 2). Additional *Ornithoptera* gynandromorphs known to the author from anecdotal reports alone have been omitted because it was impossible to independently verify their existence or the nature of their phenotype. It is hoped this paper will encourage those with gynandromorph specimens of any insect taxon to publish detailed photographs and descriptions in appropriate literature.

Acknowledgements

I am grateful to David Britton for allowing me to illustrate the *O. priamus pronomus* from the Australian Museum, and for providing its collection data. I wish also to thank Les Ring, David Rees, Ted Fenner and two anonymous reviewers, who all provided useful feedback on the draft manuscript. John Olive also provided interesting discussion regarding an additional Australian *Ornithoptera* gynandromorph. I am particularly grateful for the unwavering encouragement in all things offered by my wife, Haliz.

References

AGATE, R. J., GRISHAM, W., WADE, J., MANN, S., WINGFIELD, J., SCHANEN, C., PALOTIES A. and ARNOLD, A. 2003. Neural, not gonadal, origin of brain sex differences in a gynandromorphic finch. *Proceedings of the National Academy of Sciences* **100**: 4873-4878

BRABY, M.F. 2000. *The butterflies of Australia their identification, biology and distribution.* CSIRO Publishing: Collingwood; xx + 976 pp

BRABY, M.F. 2005. *The complete field guide to butterflies of Australia.* CSIRO Publishing: Collingwood. 2 Vols., xx + 980; 70 plates.

BRABY, M., TRUEMAN, J. and EASTWOOD, R. (2005) When and where did troidine butterflies (Lepidoptera: Papilionidae) evolve? Phylogenetic and biogeographic evidence suggests an origin in remnant Gondwana in the Late Cretaceous. *Invertebrate Systematics* **19**: 113-143.

COLLINS, N.M., and MORRIS M.G. 1985 *Threatened swallowtail butterflieds of the world: the IUCN red data handbook.* IUCN: Gland and Cambridge. viii + 402; 8 plates.

COMMON, I.F.B. and WATERHOUSE, D.F. 1981. *Butterflies of Australia. Revised edition.* Angus and Robertson: Melbourne. xiv + 684; 49 plates.

D'ABRERA, B. 2003 *Birdwing butterflies of the world. New and revised edition.* Hill House Publishers: Melbourne. 324 pp.

HANCOCK, D.L. 1983. Classification of the Papilionidae (Lepidoptera): a phylogenetic approach. *Smithersia* **2**: 1-48.

HANCOCK, D.L 1991. Notes on the phylogeny and biogeography of *Ornithoptera* Boisduval (Lepidoptera: Papilionidae). *Tyô to Ga* **42**: 17-36.

HAUGUM, J. and LOW, A.M. 1978. *A monograph on the birdwing butterflies. The systematics of Ornithoptera, Troides and related genera. Vol. 1. The genus* Ornithoptera. Scandinavian Science Press: Klampenborg. 309 pp, 12 plates.

HOWARTH, T.G. 1977. A list of the type-specimens of *Ornithoptera* (Lepidoptera: Papilionidae) in the British Museum (Natural History). *Bulletin of the British Museum (Natural History), entomology.* **36**: 153-169.

MATSUKA, H. 2001. *Natural history of birdwing butterflies.* Privately published: Japan. 368 pp.

ORR, A.G. 1988. *Mate conflict and the evolution of the sphragis in butterflies.* PhD thesis, Griffith University, Brisbane; xvii + 348 pp.

OTANI, T and KIMURA, Y. 1998. Birdwing butterflies *Ornithoptera. Endless collection series volume 7.* Endless scientific information: Japan. ii + 116 pp.

PARROTT, R.E. and SCHMID F. 1984. a new subspecies of *Ornithoptera croesus* from Morotai Island, Indonesia, and a gynandromorph of *O. croesus lydius* (Lepidoptera: Papilionidae). *The Canadian Entomologist* **116**: 1519-1524.

PARSONS, M.J. 1999. *The Butterflies of Papua New Guinea, their systematics and biology*. Academic Press: Hawaii. xvi + 738; 262 plates.

PEREIRA, R.A.S., PRADO and A.P., KJELLBERG, F. 1994. Gynandromorphism in pollinating fig wasps (Hymenoptera: Agaonidae). *Entomological News*: **114**: 152-155.

RICHARDS, O.W. and DAVIES, R.G. 1977. *Imm's general textbook of entomology. Volume 1. structure, physiology and development*. Tenth Edition. Chapman and Hall: London. PP

SANDS, D.P.A. and SCOTT, S. 2002. *Conservation of birdwing buterflies*. SciComEd and THECA: Queensland. 48 pp.

SANDS, D.P.A. and NEW, T.R. 2002. *The Action Plan for Australian Butterflies*. Environment Australia, Canberra. 378 pp.

SANDS, D.P.A., SCOTT, S.E. and MOFFATT, R. 1997. The threatened Richmond birdwing butterfly (*Ornithoptera richmondia* (Gray)): a community conservation project. *Memoirs of the Museum of Victoria* **56**: 449–453.

SCHÄFFER, O. 2001. *Butterflies of the world. Part 12 Ornithoptera*. Plates and text in two volumes. Goecke and Evers, Koltern. 14 pp. + 53 plates.

SZBAD, J., MÁTHÉ, E. and PURO, J. 1995. *Horka*, a dominant mutation of *Drosophila*, induces nondisjunction through paternal effect, chromosome loss and genetic mosaics. *Genetics* **139**: 1585-1599.

UNITED NATIONS ENVIRONMENT PROGRAMME, 2007. *Review of trade in ranched birdwing butterflies. Prepared for the European Commission Directorate*. Available online at: http://ec.europa.eu/environment/cites/pdf/review_butterflies.pdf (verified online 4 May 2010).

WIGGLESWORTH, V.B. 1972. *The principles of insect physiology. Seventh edition*. Chapman and Hall: London. viii + 827 pp.